



PREFLEDGING ENERGY REQUIREMENTS IN SHOREBIRDS: ENERGETIC IMPLICATIONS OF SELF-FEEDING PRECOCIAL DEVELOPMENT

Author(s) :Hans Schekkerman and G. Henk Visser

Source: The Auk, 118(4):944-957. 2001.

Published By: The American Ornithologists' Union

DOI: [http://dx.doi.org/10.1642/0004-8038\(2001\)118\[0944:PERISE\]2.0.CO;2](http://dx.doi.org/10.1642/0004-8038(2001)118[0944:PERISE]2.0.CO;2)

URL: <http://www.bioone.org/doi/full/10.1642/0004-8038%282001%29118%5B0944%3APERISE%5D2.0.CO%3B2>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

PREFLEDGING ENERGY REQUIREMENTS IN SHOREBIRDS: ENERGETIC IMPLICATIONS OF SELF-FEEDING PRECOCIAL DEVELOPMENT

HANS SCHEKKERMAN^{1,3,4} AND G. HENK VISSER^{2,3}

¹Alterra, P.O. Box 47, 6700 AA Wageningen, The Netherlands;

²Centre for Isotope Research, Nijenborgh 4, 9747 AG Groningen, The Netherlands; and

³Zoological Laboratory, P.O. Box 14, 9750 AA Haren, The Netherlands

ABSTRACT.—Understanding ecological consequences of avian developmental modes requires knowledge of energy requirements of chicks of different positions in the precocial–altricial spectrum, but those have rarely been measured in birds with self-feeding precocial young. We studied prefledging energy budgets in chicks of Black-tailed Godwit (*Limosa limosa*) and Northern Lapwing (*Vanellus vanellus*) in the field and in the laboratory. Lapwings show slower growth than godwits, reaching a 29% lower fledging mass (142 vs. 201 g) in a 32% longer period (33 vs. 25 days). Daily energy expenditure (DEE), measured by the doubly labelled water (DLW) technique, and daily metabolized energy (DEE plus energy deposited into tissue) increased proportionally to body mass at similar levels in both species. Total metabolized energy (TME) over the fledging period was 8,331 kJ in godwits and 6,982 kJ in lapwings, 39 and 29% higher than an allometric prediction (Weathers 1992). That suggests that self-feeding precocial chicks have high energy requirements compared with parent-fed species, due to costs of activity and thermoregulation associated with foraging. Those components made up 50–53% of TME in the shorebirds, more than twice as much as in seven parent-fed species for which DLW-based energy budgets are available. In captive lapwings and godwits growing up under favorable thermal conditions with food readily accessible, thermoregulation and activity costs were 53–58% lower and TME was 26–31% lower than in free-living chicks. The proportion of TME allocated to tissue formation (13–15% deposited as tissue plus 10–12% synthesis costs) was low in the shorebirds, and reductions in food intake may therefore sooner lead to stagnation of growth than in parent-fed chicks. Furthermore, the need to forage limits potential for saving energy by reducing activity in periods of food scarcity, because that will further decrease food intake. Self-feeding precocial chicks thus seem to operate within fairly narrow energetic margins. At the same time, self-feeding may allow birds to use food types that could not be profitably harvested if they had to be transported to the young. Received 27 March 2000, accepted 24 April 2001.

OVER THE PAST DECADES, energy expenditure and energy budgets of nestling birds have been studied in a few tens of species (reviewed by Drent et al. 1992; Weathers 1992, 1996). Interest in that field was spurred by the idea that brood size and growth rate can be seen as reproductive strategies, shaped by selection pressures such as predation risk and amount of food that parent birds can deliver to their young (Lack 1968, Ricklefs 1974, Drent and Daan 1980). Perhaps as a result, the great majority of studies of prefledging energy budgets have been conducted on species in which young are fed by their parents (e.g. 28 out of 30 studies reviewed by Weathers 1992), and very few on birds with self-feeding young. An additional reason for

scarcity of studies on self-feeding precocials may be that making necessary measurements in the field is difficult due to their mobility.

Nevertheless, knowledge of energetic requirements of precocial chicks may help understand ecological consequences of different developmental modes in the precocial–altricial spectrum (Nice 1962, Ricklefs and Starck 1998). From an energetic viewpoint, the dichotomy between parent-fed and self-feeding young may be a particularly important distinction within that spectrum. Energy expenditure of parent birds raising self-feeding young may be lower than that of birds that feed their offspring. At the same time, the burden of collecting the necessary food is shifted to the chick. That calls for an active and exposed lifestyle that can be expected to result in high energy expenditure on activity and thermoregulation.

⁴ E-mail: h.schekkerman@alterra.wag-ur.nl

Although self-feeding precocial chicks tend to grow at a slower rate than (semi)altricials (Ricklefs 1973, Ricklefs et al. 1998), and that reduces energy requirements, the savings may be limited because tissue formation is only one of several components in the budget. The net result for total energy requirements is as yet hard to judge, because the necessary measurements are lacking. If foraging leads to high energy expenditure, the scope for underestimation in laboratory studies, where food is often readily available and chicks are sheltered from adverse weather, will be particularly large in self-feeding chicks. Therefore, it is important to study energy expenditure under field conditions.

We measured energy metabolism during the pre fledging period in two shorebirds (Suborder Charadrii) with self-feeding chicks, Northern Lapwing (*Vanellus vanellus*) and Black-tailed Godwit (*Limosa limosa*). In this paper, measurements obtained in the field and in the laboratory are compared, and pre fledging energy expenditure and energy budgets are compared with those of species with parent-fed young.

METHODS

Study species.—Black-tailed Godwit and Northern Lapwing breed in a wide belt across temperate Europe and western Asia, the latitudinal range being smaller in godwits (45–62°N) than in lapwings (36–67°N). At present, most of the European populations breed in agricultural lowland wet grasslands, where densities are often higher than in the original habitat, moist natural grasslands (Hagemeijer and Blair 1997). The young feed themselves from hatching onwards, but both parents or one (some lapwings are polygynous) stay with the brood until after fledging. Godwit broods show a clear preference for tall swards (20–50 cm high) where they take small arthropods from vegetation. Lapwings are more often found on short (mown or grazed) swards, and on banks of pools and ditches, where small invertebrates are taken from the soil surface and vegetation (Beintema et al. 1991).

Field study.—Both species were studied in an area of agricultural and reserve grasslands with moderately low farming intensity near Baarn in The Netherlands (52°12'N, 5°19'E), in 1993–1995. Measurements of daily energy expenditure (DEE, kilojoules per day) were made using the doubly labelled water (DLW) method (Lifson and McClintock 1966, Nagy 1980, Speakman 1997, Visser and Schekkerman 1999). One or two chicks out of broods of three or four were captured, weighed, and injected intraper-

itoneally with 0.1 to 0.4 ml (depending on body mass) of DLW consisting of 31.1 atom percent ^2H and 62.7 atom percent ^{18}O . After an equilibration period of 1 h, four to six 10–15 μl blood samples were collected from veins in the leg (small chicks) or wing (larger ones) into glass capillary tubes, which were flame-sealed within minutes. Chicks were then released back to their family unit, and recaptured after 21.5–28.5 h (mean 24.2 ± 1.2 h), to take a second set of blood samples and determine mass change. In a small number of chicks, blood samples were also collected before injection with DLW to record background isotope levels.

Broods of Black-tailed Godwits are highly mobile and may show displacements of >1 km in a day (H. Schekkerman unpubl. data), although chicks are hard to find in the tall grass. That complicates recaptures, especially at high brood densities. Therefore, most measurements on godwits were made on broods confined to enclosures of 0.4–0.6 ha, fenced with 0.5 m high wire-netting that allowed parents but not chicks to freely leave and enter (cf. Beintema and Visser 1989a). Water but no food was provided within the enclosures, and chicks foraged on arthropods occurring naturally in vegetation. Enclosures were placed in preferred brood habitat (unmown reserve grassland), and their size was similar to the area available to wild broods at maximum observed densities in that habitat (1.7 broods/ha, H. Schekkerman unpubl. data). Behavior of enclosed godwits closely resembled that of free-living birds. Six measurements were made on free-ranging godwit chicks. Because Northern Lapwing broods are less mobile and more easily recaptured than those of godwits, all measurements were made on free-ranging young.

Weather conditions were recorded in the study area and logged every 2 min on a datalogger. Wind speed (meters per second) was measured with a calibrated anemometer at 3 m above the ground. An approximation of operative environmental temperature (T_e , °C) at chick level, which integrates air temperature and heating effect of radiation (Bakken et al. 1985, Walsberg and Weathers 1986), was measured in a blackened copper sphere of 4 cm diameter placed 10 cm above the ground. Occurrence and duration of rainfall were recorded daily.

DLW analysis.— $^2\text{H}/^1\text{H}$ and $^{18}\text{O}/^{16}\text{O}$ ratios in blood samples were analyzed with a SIRA 9 isotope-ratio mass spectrometer at the Center for Isotope Research, following procedures described in Visser and Schekkerman (1999). Analyses were done in duplicate, and a third capillary was analysed if the two measurements differed by >2%. Background concentrations were 0.0152 ± 0.00010 atom-% for ^2H and 0.2000 ± 0.00009 atom-% for ^{18}O (both $n = 6$). We calculated CO_2 -production ($r\text{CO}_2$, liters per day) according to equation 34 in Lifson and McClintock (1966), with fractionation factors k_e and k_d taken from

Speakman (1997), and a value of 0.13 for the fraction of water loss occurring by evaporation: $r\text{CO}_2 = 22.4 \times [N/2.078 \times (k_o - k_d) - 0.13 \times 0.0249 \times N \times k_d]$, in which N is the size of the body water pool (mol). This equation was derived by validating 11 DLW measurements in Northern Lapwing and Black-tailed Godwit chicks against respiration gas analysis in the laboratory (Visser and Scheckerman 1999). Relative errors of individual measurements ranged from -13 to $+16\%$, with a mean of 0% , and showed no relationship with relative growth rate of the chick during the experiment (range -17 to $+15\%$ day $^{-1}$). Those results indicate that the DLW method is applicable in shorebird chicks at a wide range of growth rates.

Because some injected isotope was sometimes lost by leakage through the puncture hole in chicks' skin, N was not estimated from isotope dilution, but from the relationship between percentage water content and fraction of adult mass attained, derived from a sample of freshly dead chicks (see below). DEE was calculated from $r\text{CO}_2$ using an energy equivalent of $27.33 \text{ kJ L}^{-1} \text{ CO}_2$ (Gessaman and Nagy 1988). Water fluxes were calculated using equation 6 of Visser and Scheckerman (1999).

Laboratory trials.—In 1986–1989, fresh eggs were obtained from breeding areas in The Netherlands and transported to the laboratory at Utrecht, where they were incubated at 37.5°C and 55 – 60% relative humidity. After hatching, chicks were housed in pairs in wooden boxes ($45 \times 60 \text{ cm}$) in a large climatic chamber at 20°C (L:D 18:6, similar to outdoor conditions). Water and food were provided *ad libitum*, whereas extra heat was provided by a 100 W infrared lamp in a corner of each box. At 1–2 weeks of age, chicks were housed in an outdoor aviary connected with an indoor section where heat (infrared lamp), water, and food were provided. Chicks were fed a pellet diet containing 28.5% crude protein. Measurements of oxygen consumption were made regularly on chicks in order to describe development of thermoregulation (Visser and Ricklefs 1993a, b).

During measurements of metabolizable energy intake (MEI, kilojoules per day) chicks were housed in pairs in wooden boxes as described above (housing chicks alone led to aberrant behavior and retarded growth). Food intake was measured over 24 h intervals by weighing the food tray and correcting for water loss. Energy content of the food was determined by bomb calorimetry, and was $19.48 \pm 0.019 \text{ kJ g}^{-1}$ dry mass ($n = 4$). At the end of each trial, we carefully collected and separated spilled food and feces. Spilled food was weighed immediately. The fecal fraction was dried for 24 h at 60°C , and weighed. Energy content of feces samples ($\sim 0.5 \text{ g}$) was determined by bomb calorimetry. Digestive efficiency for food pellets was $69.6 \pm 2.59\%$ ($n = 19$) in godwits and $55.4 \pm 1.71\%$ ($n = 11$) in lapwings, and was unrelated to chick age. Those values were used to convert crude food intake to MEI.

Carcass analysis.—Water content and energy density of growing chicks were determined by analysing composition of carcasses of five Black-tailed Godwits and three Northern Lapwings of varying ages. Chicks were killed by predators or by accident in the field ($n = 5$) or in the laboratory ($n = 3$), but had not died of starvation. Their fresh mass spanned the range found in chicks of those species, up to fledging at 70 – 80% of adult mass (Beintema and Visser 1989b). Carcasses were weighed fresh and stored in a freezer for variable periods. After thawing, they were cut into parts and dried to constant weight at 60°C to obtain dry mass. Water content (percentage) was calculated as $100 \times (\text{fresh mass} - \text{dry mass}) / \text{fresh mass}$. Soluble fat was extracted in petroleum ether during 24 h in a Soxhlet apparatus. Remains were dried for 24 h at 60°C to obtain lean dry mass. Energy density was calculated using 38 kJ g^{-1} for fat and 20 kJ g^{-1} for lean dry tissue (Ricklefs 1974). To make body-composition data comparable between species, fresh mass was expressed as a fraction of adult mass (Weathers 1996).

Energy budget.—Prefledging energy budgets were constructed on the basis of the average body mass growth curve for free-living chicks of each species in The Netherlands (Black-tailed Godwit: $M = 273 \times \exp[-\exp(-0.085 \times [a - 11.0])]$; Northern Lapwing: $M = 236 \times \exp[-\exp(0.054 \times [a - 20.5])]$, where a = age in days; Beintema and Visser 1989a), by inserting the relevant species-specific metabolic parameters at each mass. Daily metabolized energy (ME, kilojoules per day) was expressed as the sum of basal metabolism (BMR, kilojoules per day), heat loss due to assimilation of nutrients and tissue synthesis (E_{syn} , kilojoules per day), costs of thermoregulation and activity ($E_{\text{tr+act}}$, kilojoules per day), and energy deposited into new tissue (E_{tis} , kilojoules per day) (e.g. Drent et al. 1992): $\text{ME} = \text{BMR} + E_{\text{syn}} + E_{\text{tr+act}} + E_{\text{tis}}$. The first three components together constitute DEE as measured by the DLW method. BMR was not measured directly, but resting metabolic rate (RMR, kilojoules per day) of recently-fed chicks in the thermoneutral zone was determined in the laboratory-raised chicks (Visser and Ricklefs 1993a, b). Those measurements include both BMR and E_{syn} , and BMR was estimated by subtracting E_{syn} from RMR. E_{syn} was estimated as $0.78 \times E_{\text{tis}}$, based on the measured body composition and synthesis efficiencies for fat and protein in birds given by Blaxter (1989). E_{tis} was calculated as daily increment of the product of body mass and energy density.

The remaining part of DEE represents the energy allocated to thermoregulation and activity. We refrained from making separate estimates for those components (e.g. Klaassen 1994), because distinction between them is obscured by interaction effects. Physical disturbance of the insulative layer during locomotion and contact with wet vegetation are likely to elevate a foraging chick's heat loss above resting

levels. That elevation can be considered part of activity as much as of thermoregulation costs. In addition, (partial) substitution of thermoregulation costs by heat generated during activity is likely to occur (Webster and Weathers 1990, Bruinzeel and Piersma 1998).

Statistics.—Power curves for energy expenditure or water turnover as a function of body mass were fitted as linear regressions on log-transformed data. Additional explanatory variables entered (temperature, growth rate) were not log-transformed, because that would have produced impossible predictions at values ≤ 0 . Because repeated measurements on the same chick and on chicks from the same brood (or cage) do not constitute fully independent observations, variance component models were applied (Byrk and Raudenbusch 1992) that take into account that the data comprise several hierarchically nested error levels. For field measurements, factors "chick" and "brood" were treated as random effects, and for the laboratory trials, "cage." Mass, growth rate and weather variables were treated as fixed effects. The program MLWIN (Rasbash et al. 1998) was used for model fitting. Differences between godwits and lapwings in those relationships were tested by including the factor "species" (test for intercept) and interaction between species and mass (test for slope) as fixed effects in models for the combined data. Significance of explanatory variables was evaluated by likelihood ratio tests using the difference in deviance between models including and excluding the variables of interest. All tests were two-tailed, and a value of $P = 0.05$ was used to accept significance. Means are presented ± 1 SD unless indicated otherwise.

RESULTS

Carcass analysis.—Because the sample of chick carcasses was small and covariance analysis did not show significant differences between species or between wild and captive chicks, we calculated common linear regressions of energy density (ED) and water content (percentage H_2O) on the fraction of adult mass attained (M_{ad} : Northern Lapwing, 202 g [$n = 44$, $SE = 6.0$]; Black-tailed Godwit, 273 g [$n = 76$, $SE = 3.9$], mean values for both sexes in periods when no substantial fat stores are carried; H. Schekkerman unpubl. data). Energy density was related to fraction of adult mass attained as $ED = 4.38 + 3.21 \times M/M_{ad}$ ($R^2 = 0.80$, $F = 23.7$, $df = 1$ and 6 , $P = 0.003$), increasing from 4.7 kJ g^{-1} at hatching to 7.6 kJ g^{-1} at adult mass (Fig. 1A). Changes in energy density were primarily caused by changes in water content (Fig. 1B), which decreased from 79% of fresh mass

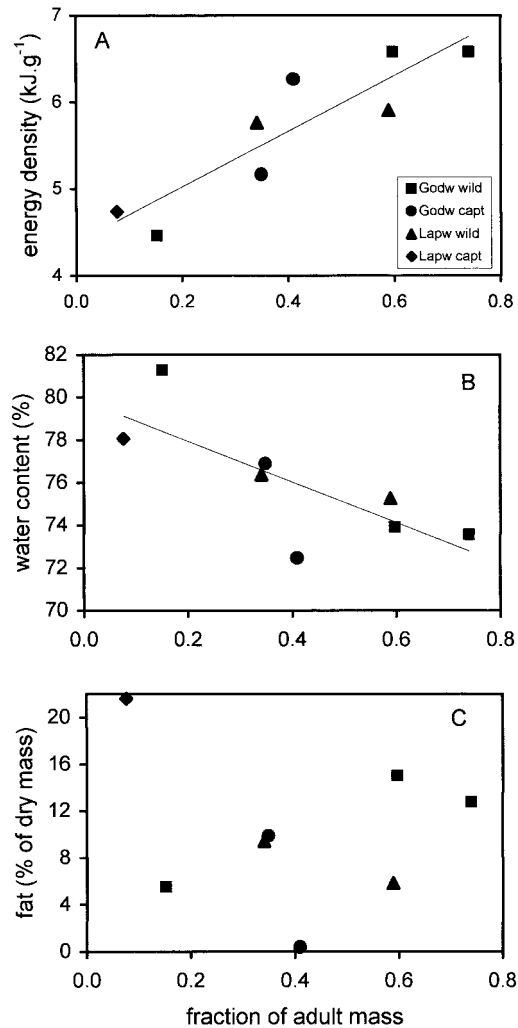


FIG. 1. Body composition of chicks in relation to fraction of adult mass attained. (A) energy density; (B) water content; (C) fat as percentage of dry mass. Symbols refer to different categories of birds. Statistics in text.

in hatchlings to 70% at adult mass (percentage $H_2O = 79.86 - 9.55 \times M / M_{ad}$; $R^2 = 0.59$, $F = 8.48$, $df = 1$ and 6 , $P = 0.027$).

There was no significant relation between fat content of carcasses and their relative mass ($F = 0.14$, $df = 1$ and 6 , $P = 0.72$), even when excluding the smallest chick with a high fat content that was probably due to residual yolk reserves ($F = 1.47$, $df = 1$ and 6 , $P = 0.28$; Fig. 1C). Disregarding that individual, the mean fat content of shorebird chicks was $7.8 \pm 4.5\%$ of total dry mass. Using that proportion and syn-

thesis efficiencies for fat and protein in birds (Blaxter 1989), synthesis costs were estimated as $E_{\text{syn}} = 0.78 \times E_{\text{tis}}$ (cf. Weathers 1996).

Energy expenditure in the field.—In total, 17 DLW measurements were made on 13 Black-tailed Godwit chicks in 8 broods; 22 measurements were made on 16 free-ranging Northern Lapwing chicks in 10 broods. A maximum of three measurements was made on a single chick, at intervals of at least four days. During measurements, godwit chicks grew between -4 and 14 g per day $^{-1}$ (mean 6.2 ± 4.7 g day $^{-1}$), which is on average $83 \pm 68\%$ (range -50 to 185%) of the mean growth rate of free-living chicks in The Netherlands at the given body mass (Beintema and Visser 1989a). That value is not significantly different from 100% ($t_{16} = 1.00$, $P = 0.16$). Lapwing chicks grew between 0 and 12.3 g day $^{-1}$ (mean 5.0 ± 3.2 g day $^{-1}$), on average $123 \pm 82\%$ (range 0 to 300%) of the mean growth rate of free-living chicks at the same mass, and again not significantly different from 100% ($t_{21} = 1.01$, $df = 21$, $P = 0.16$). We conclude that the DLW dataset was representative with respect to growth rate of chicks.

For Black-tailed Godwits, relationship between DEE and M , fitted using a variance component model, was: $DEE = 1.549 \times M^{1.092}$ (Fig. 2a; statistics in Table 1). For Northern Lapwings, it was $DEE = 2.037 \times M^{1.047}$ (Table 1). In neither species did the mass exponent differ significantly from unity (godwit, $t = 0.90$, $df = 16$, $P = 0.19$; lapwing, $t = 0.68$, $df = 21$, $P = 0.25$); hence, relationships were essentially linear. Neither the intercepts ($\chi^2 = 1.09$, $df = 1$, $P = 0.30$) nor the slopes ($\chi^2 = 1.33$, $df = 2$, $P = 0.52$) of relationships between DEE and mass differed significantly between species. Nevertheless, we used the species-specific equations for constructing energy budgets.

ME was calculated by adding E_{tis} to DEE if the animal gained weight during the DLW measurement, and set equal to DEE if no weight gain occurred. In Black-tailed Godwits, ME and body mass were related as $ME = 3.565 \times M^{0.940}$; in Northern Lapwings as $ME = 4.365 \times M^{0.911}$ (Table 2; Fig. 2b). In neither species did the mass exponent differ significantly from 1 (godwit, $t = 0.67$, $df = 16$, $P = 0.26$; lapwing, $t = 1.20$, $df = 21$, $P = 0.12$). Neither the intercepts ($\chi^2 = 1.16$, $df = 2$, $P = 0.28$) nor the slopes ($\chi^2 = 1.68$, $df = 2$, $P = 0.43$) differed significantly between the species.

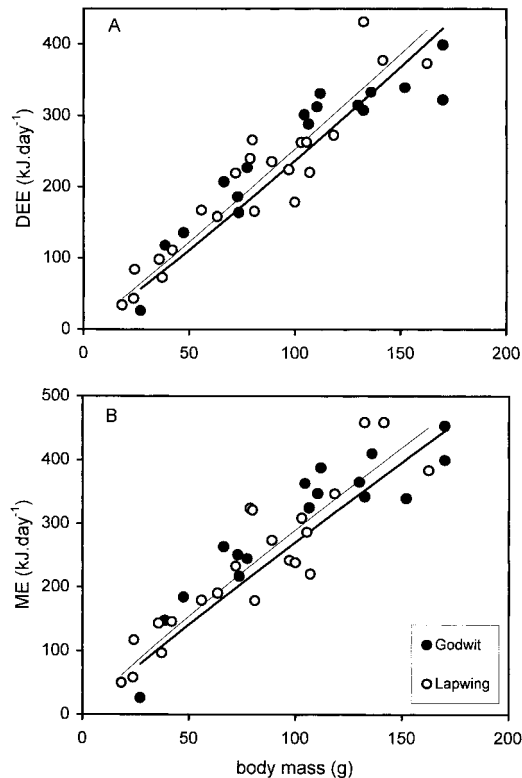


FIG. 2. Daily energy expenditure (A) and daily metabolized energy (B) in chicks of Black-tailed Godwit and Northern Lapwing in relation to body mass. Drawn lines represent the fitted allometric relationships (thick line = Godwit, thin line = Lapwing; equations in Table 1).

After allowing for effect of body mass, the remaining variation in DEE was unrelated to growth rate in both species (Black-tailed Godwit $\chi^2 = 0.79$, $df = 1$, $P = 0.37$, Northern Lapwing $\chi^2 = 1.91$, $df = 1$, $P = 0.17$). However, the residual variation in ME after allowing for body mass was positively related to growth rate in both species (Table 1), due to increasing amounts of energy deposited into tissue.

Mean operative temperature (T_e) during the 39 DLW measurements was $15.7 \pm 4.1^\circ\text{C}$ (range 7.1 – 23.5°C), close to the average T_e of 15°C measured over the period when chicks were present. Mean wind speed was 4.3 ± 1.1 m s $^{-1}$ (range 2.3 – 8.4 m s $^{-1}$). Those figures were not different between measurements on Black-tailed Godwits and Northern Lapwings ($t = 0.37$, $df = 37$, $P = 0.72$, and $t = 1.43$, $df = 37$, $P = 0.16$, respectively). Rain fell during (part

TABLE 1. Regression equations for DEE ME, and H_2O_{in} in free-living, and MEI in laboratory-raised chicks of Black-tailed Godwit and Northern Lapwing. Predictor variables used are mass (gram), operative temperature ($^{\circ}C$), and growth rate (grams per day). LRT denotes likelihood ratio test for last-included variable ($df = 1$), that is for mass in models where only mass is included, and for the "predictor" in other models.

Response variable	Predictor variable	Regression coefficients \pm SE			LRT	
		Constant	Log mass	2nd predictor	χ^2	P
Black-tailed Godwit						
log DEE	log mass	0.190 \pm 0.205	1.092 \pm 0.102	—	33.0	<0.001
	+ temperature	0.173 \pm 0.191	1.263 \pm 0.106	−0.022 \pm 0.007	5.74	0.017
log ME	log mass	0.552 \pm 0.184	0.940 \pm 0.090	—	29.5	<0.001
	+ growth rate	0.330 \pm 0.206	1.013 \pm 0.103	0.014 \pm 0.006	4.17	0.041
log H ₂ O _{in}	log mass	−0.668 \pm 0.234	1.290 \pm 0.119	—	35.9	<0.001
log MEI	log mass	0.731 \pm 0.121	0.824 \pm 0.059	—	67.5	<0.001
	+ growth rate	0.620 \pm 0.059	0.806 \pm 0.028	0.016 \pm 0.002	54.9	<0.001
Northern Lapwing						
log DEE	log mass	0.309 \pm 0.128	1.047 \pm 0.069	—	49.6	<0.001
log ME	log mass	0.640 \pm 0.137	0.911 \pm 0.074	—	43.4	<0.001
	+ growth rate	0.548 \pm 0.109	0.0911 \pm 0.057	0.018 \pm 0.005	11.1	<0.001
log H ₂ O _{in}	log mass	−0.663 \pm 0.173	1.319 \pm 0.092	—	45.1	<0.001
log MEI	log mass	0.537 \pm 0.060	0.884 \pm 0.032	—	227.2	<0.001
	+ growth rate	0.496 \pm 0.048	0.858 \pm 0.026	0.018 \pm 0.002	53.1	<0.001

of) 19 out of 39 measurement periods. In godwits, DEE decreased with operative temperature after allowing for effect of mass (Table 1). Occurrence of rainfall also affected DEE ($\chi^2 = 3.95$, $df = 1$, $P = 0.047$), but effect of wind speed was not significant ($\chi^2 = 2.46$, $df = 1$, $P = 0.12$). In lapwings, effects of operative temperature ($\chi^2 = 0.0$, $df = 1$, $P = 1.0$), wind speed ($\chi^2 = 3.64$, $df = 1$, $P = 0.06$), and rainfall ($\chi^2 = 0.07$, $df = 1$, $P = 0.79$) were not significant. Weather variables did not explain residual variation after allowing for effect of mass on ME in either species (all $P > 0.12$).

Water flux rates.—Daily water influx of Black-tailed Godwit chicks (H_2O_{in} , grams per day) was related to body mass as: $H_2O_{in} = 0.215 \times M^{1.290}$, of Northern Lapwing chicks as $H_2O_{in} = 0.217 \times M^{1.319}$ (Table 1). Intercepts ($\chi^2 = 1.60$, $df = 2$, $P = 0.21$) and slopes ($\chi^2 = 2.25$, $df = 2$, $P = 0.32$) were not significantly different for the

two species. Water influx rates in chicks were markedly higher than predicted from a mass-based allometric relationship for adult wild birds in the field (Nagy and Peterson 1988): the mean difference was $+146 \pm 72\%$ ($n = 17$) for godwits, and $+141 \pm 87\%$ ($n = 22$) for lapwings.

Field energy budgets.—Total energy requirements of Northern Lapwings and Black-tailed Godwits increased throughout the pre fledging period, without a maximum or plateau before fledging as found in several altricial and semi-precocial birds (Fig. 3). ME reached the highest value (godwit, 556 kJ day^{-1} , lapwing 399 kJ day^{-1}) at fledging, but probably still further increases thereafter because chicks continue growing for some time (Beintema and Visser 1989b). Taking age of fledging (25 days for godwits, 33 days for lapwings; H. Schekkerman unpubl. data) as a natural endpoint for inter-

TABLE 2. Comparison of estimated TME and E_{t+act} of godwit and lapwing chicks growing up at identical growth rates in the field and in the laboratory.

Species	Energetic parameter	Field (kJ)	Laboratory (kJ)	Savings in laboratory	
				Field-lab (kJ)	(Field-lab)/field (%)
Black-tailed Godwit	TME	8331	6166	2165	25.9
	E_{t+act}	4124	1959	2165	52.5
Northern Lapwing	TME	6982	4832	2150	30.8
	E_{t+act}	3688	1538	2150	58.3

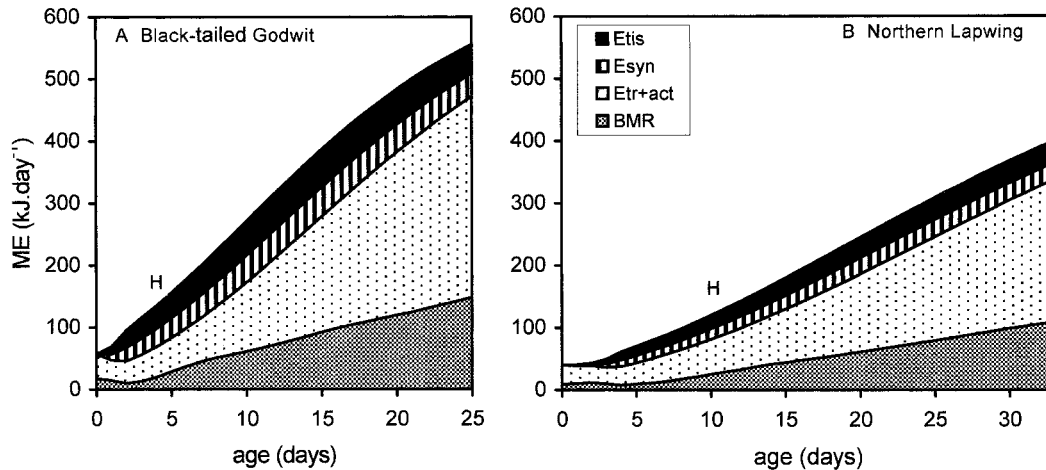


FIG. 3. Prefledging energy budgets for free-living Black-tailed Godwits and Northern Lapwings growing at the average rate, from hatching to fledging. Components shown are BMR, E_{syn} , $E_{\text{tr+act}}$ and E_{tis} . "H" denotes the age at which homeothermy is achieved at 10°C (from Visser and Ricklefs 1993b).

specific comparisons, total metabolized energy over that period (TME) amounted to 8,331 kJ in godwits and 6,982 kJ in lapwings. Average daily metabolized energy (ADME), which is TME divided by both fledging mass (godwit 201 g, lapwing 142 g) and time to fledging (Weathers 1992), was $1.66 \text{ kJ g}^{-1} \text{ day}^{-1}$ in godwits and $1.49 \text{ kJ g}^{-1} \text{ day}^{-1}$ in lapwings.

The allocation of energy to different components of the budget was very similar in the two species (Fig. 3). Proportion of TME made up by E_{tis} was estimated at 15% in Black-tailed Godwits and 13% in Northern Lapwings. Resting metabolism amounted to 35% of total energy requirements in both species, of which ~24% was estimated to be basal metabolism and 11% synthesis costs. The remaining part of TME (50 and 53%) was spent on thermoregulation and activity.

Energy expenditure in the laboratory.—Captive Northern Lapwing chicks achieved a mean growth rate of $4.9 \pm 2.3 \text{ g day}^{-1}$ (range 0.3 to 11.3 g day^{-1} , $n = 114$) during food intake trials, similar to the birds in the DLW sample and slightly higher than the average for Dutch chicks in the field. In contrast, the lab-raised Black-tailed Godwits grew on average $8.7 \pm 4.1 \text{ g day}^{-1}$ (range 2– 19.7 g day^{-1} , $n = 48$), which is 40% more than chicks subjected to DLW measurements in the field and also more than the average free-living chick.

MEI of laboratory-raised Black-tailed Godwit chicks was related to body mass as: $\text{MEI} =$

$5.382 \times M^{0.824}$; in Northern Lapwings this relationship was: $\text{MEI} = 3.444 \times M^{0.884}$ (Table 1). In both species, growth rate explained a significant part of the residual variation in MEI after including body mass (Table 1).

MEI of captive Black-tailed Godwits was similar to ME found in the field up to ~100 g, but fell behind at higher body masses. In Northern Lapwing chicks, it was markedly lower in the laboratory than in the field at all masses (Fig. 4). In view of differences in growth rate between laboratory and field chicks, energy budgets for those groups were made comparable by inserting average growth of free-living chicks into the equation relating MEI to mass and growth rate (see Table 1). The resulting estimates of total MEI over the pre-fledging period were 26 and 31% lower in godwits and lapwings, respectively, than TME values obtained with DLW in the field. Because at the same growth rate BMR, E_{syn} and E_{tis} can be assumed equal in the field and in captivity, difference must be due to thermoregulation and activity costs. Estimated total $E_{\text{tr+act}}$ up to fledging was 53 and 58% lower in the laboratory than in the field for lapwings and godwits respectively (Table 2).

DISCUSSION

General.—To our knowledge, this study is the first to measure energy metabolism of self-feeding precocial chicks in the field. Below, we

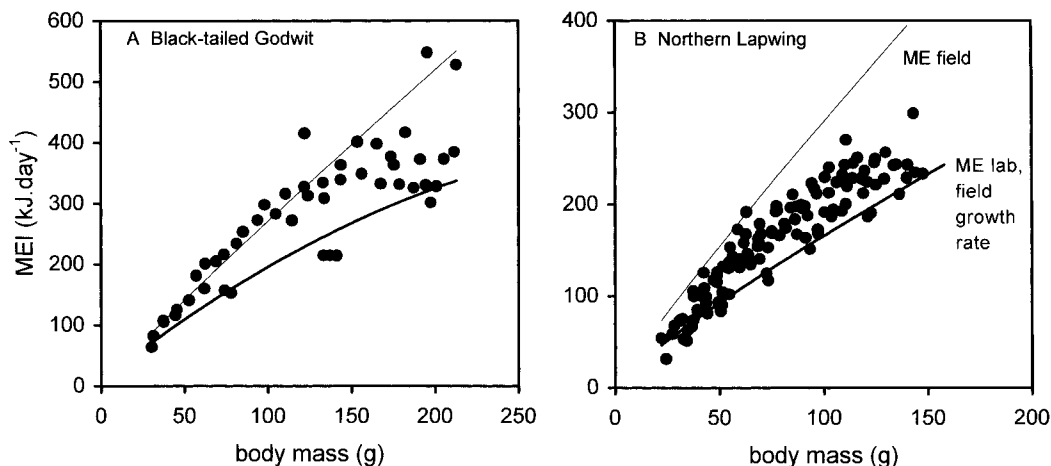


FIG. 4. MEI (dots) of laboratory-raised chicks of Black-tailed Godwit (A) and Northern Lapwing (B) in relation to body mass. Continuous lines indicate the expected ME of chicks in the field (thin) and the expected MEI of laboratory chicks growing at the same rate as chicks in the field (thick).

compare those estimates with data for other bird species, as a first test of the idea that the active and exposed lifestyle of self-feeding precocials leads to high energy requirements. That idea also predicts that proportion of TME allocated to E_{tr+act} is relatively large in that group. We also discuss that E_{tr+act} is likely to be underestimated in captivity, so that it is important to make comparisons on the basis of data obtained in the field. The fact that field measurements in godwits were made in enclosures did not affect their energy budgets in such a way that growth rates during DLW trials significantly differed from those of free-living chicks. All measurements in Northern Lapwings were made on free-living chicks.

Weathers (1992) discussed accuracy of estimates of pre fledging energy requirements, which consist of several separately estimated components. He concluded that estimates based on respirometry or food consumption experiments may involve errors of $\pm 25\%$, but that errors in studies using doubly labelled water (DLW) are smaller, usually less than $\pm 8\%$. Schekkerman and Visser (1999) found an average discrepancy of $\pm 8.1\%$ between simultaneous measurements obtained using DLW and respiration gas analysis in captive godwit and lapwing chicks. Because daily energy expenditure (DEE), as measured with DLW, makes up 85–87% of TME in chicks in the field, estimation of E_{tis} (error $\sim 5\%$) contributes little to

errors in TME, which therefore will be also close to $\pm 8\%$. Because coefficients of variation for estimates of gross energy content of the food (0.1%), and for the digestive efficiencies (3.7 and 3.1% for Black-tailed Godwit and Northern Lapwing respectively, see above) are low, average random error in the MEI estimates for lab-raised chicks will probably be $< 5\%$.

Body composition of precocial young.—Precocial and semiprecocial birds hatch with greater locomotory and thermoregulatory abilities than altricials, reflected in functionally more mature tissues with a lower water content (Ricklefs 1983, Starck and Ricklefs 1998). Because water content and energy density (ED) of tissue are inversely related, precocials and semiprecocials should show higher ED at hatching than altricials (Ricklefs 1974). In line with that, the intercepts of regression equations relating ED to fraction of adult mass for six semiprecocial birds (mean 4.03 ± 0.23) listed in a review by Weathers (1996) are significantly higher than for the 10 altricials (2.92 ± 0.45 , $t = 5.55$, $df = 14$, $P < 0.001$). The only precocial included, the Japanese Quail (*Coturnix coturnix*), showed the highest intercept (4.39), similar to the value for shorebird chicks (4.38).

Because adult body composition is not affected by developmental mode, a high intercept should lead to a shallower slope in (semi)precocial young (Ricklefs 1974). That difference is not significant in Weathers'

(1996) dataset however, (altricials 5.03 ± 0.96 , semiprecocials 4.67 ± 0.51 ; $t = 0.84$, $df = 14$, $P = 0.41$), perhaps because of deposition of pre fledging fat stores in the semiprecocial seabirds included. Shorebird chicks did not lay down such stores, and the large intercept and shallow slope found in the carcass analysis thus conform to expectation.

Differences between lapwings and godwits.—Despite the fact that fledging mass of Northern Lapwings was 29% lower than in Black-tailed Godwits, TME over the pre fledging period was only 16% lower. That was due to the fact that young lapwings fledged at a 32% older age than godwits, causing costs of basal metabolism, thermoregulation, and activity to accrue over a longer period.

Slow growth has been interpreted as a mechanism to reduce daily energy requirements, thus alleviating the daily work load of the parents (e.g. Lack 1968, Drent and Daan 1980) or, in self-feeding precocials, the chicks. Besides a direct saving through reduction of tissue formation, there may be an additional saving if basal metabolism is coupled to growth rate, as hypothesized by Drent and Klaassen (1989) and Klaassen and Drent (1991). Indeed, over much of the pre fledging period, mass-specific RMR in the thermoneutral zone is lower in young Northern Lapwings than in chicks of both the larger Black-tailed Godwit and the smaller Ruff (*Philomachus pugnax*) and Redshank (*Tringa totanus*; Visser and Ricklefs 1993a). Those three species belong to the Scolopacidae (sandpipers), which grow faster than plovers and lapwings (Charadriidae; Beintema and Visser 1989b). It has been suggested that the slower growth of plovers may be related to an evolutionary past in semiarid regions, warmer but generally poorer in food than boreal marshes and tundras where most Scolopacidae occur. That would make a reduction of metabolism and growth rate both climatically permissible and energetically advantageous (Beintema and Visser 1989a). In contrast, the high-latitude provenance of sandpipers, through a short season suitable for reproduction, may have selected for rapid growth (Carey 1986, Schekkerman et al. unpubl. data) at the expense of higher energy requirements.

Despite differences in growth rate and RMR, mass-specific daily energy expenditure and

metabolized energy did not differ significantly between free-living Northern Lapwings and Black-tailed Godwits, and average daily metabolized energy (ADME) differed by only 10%. Either the lapwings' savings on growth and resting metabolism were obscured by sampling variation, or they were offset by increased expenditure on other components of the budget. Because minimal thermal conductance does not differ between lapwings and godwits at the same mass (Visser and Ricklefs 1993b), that could be due to differences in the thermal environment (e.g. amount of shelter) or foraging activity. Because we estimated thermoregulation and activity costs jointly and by subtraction of the other budget components from ME, we are unable to unravel that further.

Energetic costs of self-feeding precociality.—Weathers (1992) reviewed data on pre fledging energy requirements for 30 bird species (20 [semi]altricials, 8 semiprecocials, and 2 precocials; mostly from the temperate zone), and found that total energy metabolized over the fledging period increases with both body mass and age at fledging, the average deviation of observed from predicted values being only $\pm 14\%$. TME of Black-tailed Godwits (8,331 kJ) and Northern Lapwings (6,982 kJ) was 39 and 29% higher than predicted by that relationship (6,004 and 5,422 kJ respectively). That difference is larger than the potential error in TME estimates (approximately 8–25%; Weathers 1992). Estimates of average daily metabolized energy per gram of fledgling produced (ADME, 1.66 and 1.49 $\text{kJ g}^{-1} \text{day}^{-1}$ for godwits and lapwings, respectively) were 54 and 27% above Weathers' (1992) predictions (1.08 and 1.17 $\text{kJ g}^{-1} \text{day}^{-1}$). The value for godwits differed more from the prediction than those for any of the 30 species listed. Finally, the highest values of ME found before fledging (peak DME, 556 and 399 kJ day^{-1}) were 53 and 69% above allometric predictions (364 and 236 kJ day^{-1} ; Weathers 1992). Fledging age of lapwings and godwits is within the range found in similar-sized species in Weathers's sample, so those comparisons do not involve extrapolations.

Hence, Black-tailed Godwit and Northern Lapwing chicks show high energy requirements compared to other birds for which data are available. That is probably due to their self-feeding lifestyle, involving much locomotor ac-

tivity and high thermoregulation costs because of the need to forage outside the shelter of a nest. If so, high energy requirements should be a general characteristic of self-feeding precocial chicks, especially in temperate and cold climates, and the activity–thermoregulation component of the energy budget should be large in that group compared to parent-fed birds. Estimates of TME in captive self-feeding young ducks and quails (Sugden and Harris 1972, Cain 1976, Blem 1978, Blem and Zara 1980) are between 18% lower and 5% higher than the allometric predictions, but those studies are likely to have underestimated field metabolism as food was available *ad libitum*, and holding facilities were generally heated and sometimes restricted locomotor activity (see below). Norton's (1973) estimate of TME in Dunlins (*Calidris alpina*) raised indoors is only 1% above the allometric prediction, but he estimated that free-living chicks in the Alaskan tundra would require 40% (Norton 1970) to 100% (Norton 1973) more energy. Recent field measurements using DLW in another Arctic shorebird, the Knot (*Calidris canutus*), revealed a TME that was 89% above the predicted value (Schekkerman et al. unpubl. data). Those high values probably reflect interaction of precociality with the cold Arctic environment.

In Black-tailed Godwits and Northern Lapwings, 50–53% of TME was allocated to E_{tr+act} . Those proportions can be compared to those in three altricial and four semiprecocial species for which DLW-based field energy budgets are available (Fig. 5). All those studies assumed a synthesis efficiency of 75% (Ricklefs 1974), a value that is considered too high by some workers (e.g. Weathers 1996; but see Konarzewski 1995, Ricklefs et al. 1998). Because E_{tr+act} is found by subtracting BMR and E_{syn} from DEE, underestimation of E_{syn} leads to overestimation of E_{tr+act} . Recalculation of E_{tr+act} for the seven parent-fed species, using efficiency estimates according to Blaxter (1989), results in proportions of TME averaging $19 \pm 6\%$ (range 12–30%, $n = 8$). Uncorrected values averaged $26 \pm 6\%$ (range 18–36%), still only half the value in the shorebirds.

High thermoregulation and activity costs in shorebird chicks agree with observations on their time-activity budgets (H. Schekkerman unpubl. data). Black-tailed Godwit chicks in the field spend 7–16 h per day (50–90%, average

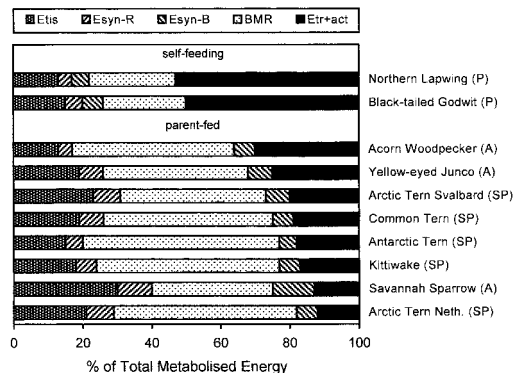


FIG. 5. Prefledging energy budgets for Black-tailed Godwit and Northern Lapwing in the field and in the laboratory (this study), compared with DLW-based field budgets for Acorn Woodpecker (*Melanerpes formicivorus*; Weathers et al. 1990), Yellow-eyed Junco (*Junco phaeonotus*; Weathers and Sullivan 1991), Arctic Tern (*Sterna paradisaea*; Spitsbergen, Klaassen et al. 1989; Netherlands, Klaassen 1994), Common (*S. hirundo*) and Antarctic (*S. vittata*) terns (Klaassen 1994), kittiwake (*Rissa tridactyla*; Gabrielsen et al. 1992), and Savannah Sparrow (*Passerculus sandwichensis*; Williams and Prints 1986). Acronyms denote ontogenetic types: P = precocial, SP = semiprecocial, A = altricial. Species are ordered according to the proportion of total metabolism allocated to E_{tr+act} . E_{syn-B} denotes the increase in the estimate of synthesis costs above that based on a synthesis efficiency of 75% (E_{syn-R}) caused by using synthesis efficiencies from Blaxter (1989). In the shorebird budgets, that difference led to a lower estimate of BMR; in the other species, to a lower estimate of E_{tr+act} .

80%, of the 16 h daylight period in chicks older than a week) actively searching for prey, walking distances of 4–10 km day⁻¹. Northern Lapwing chicks receive more parental brooding than godwits (Beintema and Visser 1989a), but chicks ≥ 7 days old spend $\sim 70\%$ of the daylight period actively foraging. In contrast, chicks of the semiprecocial Common and Arctic terns, even when hardly brooded anymore at ages ≥ 15 days, allocate $< 20\%$ of the daylight period to activity (Klaassen et al. 1994). Altricial House Wren (*Troglodytes aedon*) nestlings 6–10 days old spend even less time on active behaviors (shivering, small movements, and begging): 4–8% of the 14 h day (Bachman and Chappell 1998).

Energy requirements in laboratory and field.—If thermoregulation and foraging cause the high energy expenditure in free-living shorebird

chicks, it can be expected that metabolism is reduced in the laboratory, where chicks are not exposed to cold and wind and food is available without effort. The scope for saving energy in captivity would be larger in self-feeding precocials than in altricials and semiprecocials with lower natural activity levels. In line with that, ME of the laboratory-raised shorebirds was generally lower than that of free-ranging chicks at the same mass. After correcting for growth rate differences, E_{tr+act} was estimated 53–58% lower in the lab than in the field, resulting in a 26–31% lower TME (Table 2). Nevertheless, the savings in captive shorebirds were not much larger than the 25% difference between field and laboratory ME reported for altricial Savannah Sparrows by Williams and Prints (1986). Their measurements of oxygen consumption in small metabolic chambers at thermoneutrality probably included negligible E_{tr+act} whereas that component was still substantial during our food intake trials. Had E_{tr+act} been negligible in captive shorebird chicks, the difference with field metabolism would have been 50–53%. We conclude that laboratory measurements are likely to substantially underestimate energy requirements especially in self-feeding precocial chicks.

Ecological implications of self-feeding precociality.—Compared to parent-fed nestlings of similar size, young shorebirds need to ingest more food to sustain themselves. In addition, their lifestyle does not provide much leeway in periods of food scarcity. Because foraging is by far the most important form of activity, shorebird chicks cannot save energy by reducing activity, as observed in semiprecocial terns (Klaassen et al. 1994), without further reducing food intake. Only if food intake rate falls below concomitant energy expenditure should chicks stop foraging. They might save some energy by selecting sheltered microhabitats (Wiersma and Piersma 1994), but potential savings are probably small. Even in good conditions, Black-tailed Godwits forage mostly in tall grass, where wind influence is much reduced (Klaassen 1994); variation in wind speed at 3 m height had no discernible effect on DEE in godwits. Hence, they can hardly find more shelter when conditions deteriorate. In addition, reduced food availability for young of both species is often associated with windy and cold or wet weather (H. Schekkerman unpubl. data),

and will thus tend to coincide with increased thermoregulation costs due to low temperature or rain, which may offset any savings due to wind shelter. Chicks may also compensate for a reduced foraging yield by increasing foraging time, but because they already spend most (~80%) of the daylight period foraging under normal conditions, scope for that is limited, and it is further reduced when chicks need to be brooded more often during cold weather (Beintema and Visser 1989a).

If basal metabolism, activity, and thermoregulation cannot be substantially economized upon, it is inevitable that energy shortage soon results in reductions in growth rate. Proportion of TME that is allocated to growth ($E_{tis} + E_{syn}$) is comparatively small in the shorebirds: 23–27%, compared to 24–52% (mean 33%), in the seven altricials or semiprecocials in Figure 5 (note that under the alternative assumption of 75% synthesis efficiency, proportion of TME allocated to growth is only 17–20% in the shorebirds). That implies that small reductions in energy intake may lead to stagnation of growth. Our data further show that shorebird chicks do not carry substantial fat deposits that enable them to overcome long periods of food scarcity: a two-week old, 126 g godwit chick carries ~10 g of fat, which is enough to sustain its normal DEE for 1.3 days. Those points suggest that self-feeding shorebird chicks operate within fairly narrow energetic margins, and therefore depend on a reliable food supply for successful development.

Conversely, parents of self-feeding precocials do not have to spend time and energy procuring and transporting food to their young. Although field measurements of energy expenditure in parent birds tending self-feeding chicks are still too scarce to reveal patterns, it seems likely that they will be lower than those of birds that do feed their young, if only because costly flights with food are unnecessary. In addition, precocial parents may be less time-limited, because feeding for their own needs is more compatible with guarding a brood than with collecting food for them. Thus, parents are partially relieved from one of the most energetically stressful periods in the annual cycle (Drent and Daan 1980, Tatner and Bryant 1993), and that may enhance their survival or future fecundity (Daan et al. 1996, Golet et al. 1998).

From a chick's viewpoint, the need to transport food is costly too, because profitability of prey is reduced by time lost on transportation. The extent of that reduction decreases with energetic yield of the load (and increases with transportation distance). Hence, unless multiple-prey loading is possible, transporting food to young is especially unprofitable, shifting the evolutionary balance towards self-feeding, when prey are of low energetic value, or small relative to body size. At the same time, capturing large and energy-rich prey may often require strength and skills not present in small young (Nice 1962, Ricklefs and Starck 1998). Those points may explain why self-feeding is common in young of herbivorous birds (geese, some gamebirds; low-energy food) and among medium-sized species that feed on invertebrates that occur in high densities but are of small size (ducks, shorebirds, and gamebirds). A further energetic advantage of self-feeding for chicks is that scramble competition for food between brood mates can be largely avoided, although interference competition may still occur.

Conclusion.—The limited data available to date suggest that a high energy expenditure on activity and thermoregulation associated with foraging in self-feeding shorebird chicks makes that mode of development energetically costly. Field measurements on shorebirds that are fed by their parents (oystercatchers, stone-curlews, snipes), and on species in other self-feeding precocial taxa like Anseriformes and Galliformes, are needed to confirm that pattern is unique to, and general among, birds with self-feeding young. Such measurements will also provide an empirical basis for models for exploring relative performance of self-feeding and parental feeding under different conditions of climate and food availability, which may shed some light on evolution of avian developmental modes. In such models, it is important to consider the family unit as a whole, which means that measurements of energy expenditure in parent birds tending self-feeding young are also called for.

ACKNOWLEDGMENTS

We thank Arjen Boele, Karen Krijgsveld, Martjan Lammertink, Suzan van Lieshout, Jeroen Postema, Nelly Swijnenburg, Ingrid Tulp and Odette Vervoort for assistance in the field. T. Dijkstra and B. Verstap-

pen-Dumoulin conducted the isotope analyses. Albert Beintema supported the study in various ways throughout. The manuscript was improved thanks to comments by Albert Beintema, Rudolf Drent, Arie Spaans, Eric Stienen, and Ingrid Tulp. This study was supported by the Dienst Landelijk Gebied of the Dutch Ministry of Agriculture, Nature Management and Fisheries. Permission to work in the meadow-bird reserve at Baarn was granted by "Natuurmonumenten" (R. Niewerf) and by several land owners, notably P. van Rossenberg, who also hospitably provided a working base.

LITERATURE CITED

- BACHMAN, G. C., AND M. A. CHAPPELL. 1998. The energetic cost of begging behaviour in nestling House Wrens. *Animal Behavior* 55:1607–1618.
- BAKKEN, G. S., W. R. SANTEE, AND D. J. ERSKINE. 1985. Operative and standard operative temperature: Tools for thermal energetics studies. *American Zoologist* 25:933–934.
- BEINTEMA, A. J., AND G. H. VISSER. 1989a. The effect of weather on time budgets and development of meadow birds. *Ardea* 77:181–192.
- BEINTEMA, A. J., AND G. H. VISSER. 1989b. Growth parameters in chicks of charadriiform birds. *Ardea* 77:169–180.
- BEINTEMA, A. J., J. B. THISSEN, D. TENSEN, AND G. H. VISSER. 1991. Feeding ecology of charadriiform chicks in agricultural grassland. *Ardea* 79:31–44.
- BLAXTER, K. 1989. *Energy Metabolism in Animals and Man*. Cambridge University Press, Cambridge, United Kingdom.
- BLEM, C. R. 1978. The energetics of young Japanese Quail, *Coturnix coturnix japonica*. *Comparative Biochemistry and Physiology A* 59:219–223.
- BLEM, C. R., AND J. ZARA. 1980. The energetics of young bobwhite (*Colinus virginianus*). *Comparative Biochemistry and Physiology A* 67:611–615.
- BRUINZEEL, L. W., AND T. PIERSMA. 1998. Cost reduction in the cold: Heat generated by terrestrial locomotion partly substitutes for thermoregulation costs in Knot *Calidris canutus*. *Ibis* 140:324–328.
- BYRK, A. S., AND S. W. RAUDENBUSH. 1992. *Hierarchical Linear Models, Application and Data Analysis*. Sage, London.
- CAIN, B. W. 1976. Energetics of growth for Black-bellied Tree Ducks. *Condor* 78:124–128.
- CAREY, C. 1986. Avian reproduction in cold climates. Pages 2708–2715 in *Acta XIX Congressus Internationalis Ornithologici* (H. Ouellet, Ed.). Natural Museum of Natural Sciences, Ottawa, Ontario.
- DAAN, S., C. DEERENBERG, AND C. DIJKSTRA. 1996. Increased daily work precipitates death in the Kestrel. *Journal of Animal Ecology* 65:539–544.

- DRENT, R. H., AND S. DAAN. 1980. The prudent parent: Energetic adjustments in avian breeding. *Ardea* 68:225–252.
- DRENT, R. H., AND M. KLAASSEN. 1989. Energetics of avian growth: The causal link with BMR and metabolic scope. Pages 249–359 in *Physiology of Cold Adaptation in Birds* (C. Bech and R. E. Reinertsen, Eds.). Plenum, New York.
- DRENT, R. H., M. KLAASSEN, AND B. ZWAAN. 1992. Predictive growth budgets in terns and gulls. *Ardea* 80:5–17.
- GABRIELSEN, G. W., M. KLAASSEN, AND F. MEHLUM. 1992. Energetics of Black-legged Kittiwake *Rissa tridactyla* chicks. *Ardea* 80:9–40.
- GESSAMAN, J. A., AND K. A. NAGY. 1988. Energy metabolism: Errors in gas-exchange conversion factors. *Physiological Zoology* 61:07–513.
- GOLET, G. H., D. B. IRONS, AND J. A. ESTES. 1998. Survival costs of chick rearing in Black-legged Kittiwakes. *Journal of Animal Ecology* 67:827–841.
- HAGEMEIJER, E. J. M., AND M. J. BLAIR. 1997. EBCC Atlas of European Breeding Birds. T. and A. D. Poyser, London.
- KLAASSEN, M. 1994. Growth and energetics of tern chicks from temperate and polar environments. *Auk* 111:525–544.
- KLAASSEN, M., C. BECH, D. MASMAN, AND G. SLAGSVOLD. 1989. Growth and energetics of Arctic Tern chicks (*Sterna paradisaea*). *Auk* 106:240–248.
- KLAASSEN, M., AND R. H. DRENT. 1991. An analysis of hatchling resting metabolism: In search of ecological correlates that explain deviations from allometric relations. *Condor* 93:612–629.
- KLAASSEN, M., B. HABEKOTTÉ, P. SCHINKELSHOEK, E. STIENEN, AND P. VAN TIENEN. 1994. Influence of growth rate retardation on time budgets and energetics of Arctic Tern *Sterna paradisaea* and Common Tern *S. hirundo* chicks. *Ibis* 136:197–204.
- KONARZEWSKI, M. 1995. Allocation of energy to growth and respiration in avian postembryonic development. *Ecology* 76:8–19.
- LACK, D. 1968. *Ecological Adaptations for Breeding in Birds*. Methuen, London.
- LIFSON, N., AND R. MCCLINTOCK. 1966. Theory of use of the turnover rates of body water for measuring energy and material balance. *Journal of Theoretical Biology* 12:46–74.
- NAGY, K. A. 1980. CO₂-production in animals: Analysis of potential errors in the doubly labelled water method. *American Journal of Physiology* 238:R466–R473.
- NAGY, K. A., AND S. C. PETERSON. 1988. *Scaling of water flux rate in animals*. University of California Publications in Zoology vol. 120.
- NICE, M. M. 1962. Development of behavior in precocial birds. *Transactions of the Linnaean Society of New York* 8:1–211.
- NORTON, D. W. 1970. Thermal regimes of nests and bioenergetics of chick growth in the Dunlin (*Calidris alpina*) at Barrow, Alaska. M.S. thesis, University of Alaska, Fairbanks.
- NORTON, D. W. 1973. Ecological energetics of calidridine sandpipers breeding in northern Alaska. Ph.D. dissertation, University of Alaska, Fairbanks.
- RASBASH, J., M. HEALY, W. BROWNE, AND B. CAMERON. 1998. MLwiN version 1.00. Multilevel Models Project. Institute of Education, University of London, London.
- RICKLEFS, R. E. 1973. Patterns of growth in birds. II. Growth rate and mode of development. *Ibis* 115:177–201.
- RICKLEFS, R. E. 1974. Energetics of reproduction in birds. Pages 152–292 in *Avian Energetics* (R. A. Paynter, Ed.). Publications of the Nuttall Ornithological Club, no. 15.
- RICKLEFS, R. E. 1983. Avian postnatal development. Pages 1–83 in *Avian Biology*, vol. 7 (D. S. Farner, J. R. King, and K. C. Parkes, Eds.). Academic Press, New York.
- RICKLEFS, R. E., AND J. M. STARCK. 1998. The evolution of the developmental mode in birds. Pages 366–380 in *Avian Growth and Development* (J. M. Starck and R. E. Ricklefs, Eds.). Oxford University Press, New York.
- RICKLEFS, R. E., J. M. STARCK, AND M. KONARZEWSKI. 1998. Internal constraints on growth in birds. Pages 266–287 in *Avian Growth and Development* (J. M. Starck and R. E. Ricklefs, Eds.). Oxford University Press, New York.
- SPEAKMAN, J. R. 1997. *Doubly Labelled Water. Theory and Practice*. Chapman and Hall, London.
- SUGDEN, L., AND L. E. HARRIS. 1972. Energy requirements and growth of captive Lesser Scaup. *Poultry Science* 51:625–633.
- STARCK, J. M., AND R. E. RICKLEFS. 1998. Patterns of development: The altricial–precocial spectrum. Pages 3–30 in *Avian Growth and Development* (J. M. Starck and R. E. Ricklefs, Eds.). Oxford University Press, New York.
- TATNER, P., AND D. M. BRYANT. 1993. Interspecific variation in daily energy expenditure during avian incubation. *Journal of Zoology (London)* 231:215–232.
- VISSER, G. H., AND R. E. RICKLEFS. 1993a. Temperature regulation in neonates of shorebirds. *Auk* 110:445–457.
- VISSER, G. H., AND R. E. RICKLEFS. 1993b. Development of temperature regulation in shorebirds. *Physiological Zoology* 66:771–792.
- VISSER, G. H., AND H. SCHEKKERMAN. 1999. Validation of the doubly labelled water method in growing precocial birds: The importance of assumptions concerning evaporative water loss. *Physiological and Biochemical Zoology* 72:740–749.

- WALSBERG, G. E., AND W. W. WEATHERS. 1986. A simple technique for estimating operative environmental temperature. *Journal of Thermal Biology* 11:67–72.
- WEATHERS, W. W. 1992. Scaling nestling energy requirements. *Ibis* 134:142–153.
- WEATHERS, W. W. 1996. Energetics of postnatal growth. Pages 461–496 in *Avian Energetics and Nutritional Ecology* (C. Carey, Ed.). Chapman and Hall, New York.
- WEATHERS, W. W., W. D. KOENIG, AND M. T. STANBACK. 1990. Breeding energetics and thermal ecology of the Acorn Woodpecker in central coastal California. *Condor* 92:341–359.
- WEATHERS, W. W., AND K. A. SULLIVAN. 1991. Growth and energetics of nestling Yellow-eyed Juncos. *Condor* 93:138–146.
- WEBSTER, M. D., AND W. W. WEATHERS. 1990. Heat produced as a byproduct of foraging activity contributes to thermoregulation by Verdins *Auriparus flaviceps*. *Physiological Zoology* 63:777–794.
- WIERSMA, P., AND T. PIERSMA. 1994. Effects of microhabitat, flocking, climate and migratory goal on energy expenditure in the annual cycle of Red Knots. *Condor* 96:257–279.
- WILLIAMS, J. B., AND A. PRINTS. 1986. Energetics of growth in nestling Savannah Sparrows: A comparison of doubly-labelled water and laboratory estimates. *Condor* 88:74–43.

Associate Editor: C. Blem